DEVELOPMENT OF DIATOM COMMUNITIES ON POTAMOGETON ROBBINSII OAKES

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One of the most important groups of organisms in the aquatic system is the periphyton, the organisms that grow attached to macrophytes, logs, rocks, mud or other submersed objects. Periphyton species which are primarily composed of Bacillariophyceae (diatoms) are often found in large numbers producing slimy mats (Young, 1945). The periphyton are important in overall lake productivity (Wetzel, 1964), and recently have been used as tools in studying critical environmental problems (Rashke & Weber, 1970; Baker, 1974). Despite the importance of periphyton in aquatic systems and their usefulness as environmental tools, there has been much neglected research. The objective of this study was to broaden the information regarding periphyton ecology.

The attached diatom communities on *Potamogeton robbinsii* Oakes, a submerged pondweed, were observed throughout 1975 in Wheelwright Pond in Lee, New Hampshire. The communities were qualitatively and quantitatively described from leaves along various intervals of the shoot. Seasonal fluctuations in concentrations of the diatom species were observed. Temporal changes in community composition were also observed on *P. robbinsii* leaves. Whitford (1959) developed a method to study pioneer versus climax communities of diatoms by comparing the attached communities on young and old parts of vertically-oriented aquatic plants. In this study the influence of depth was eliminated because *P. robbinsii* grows parallel to the bottom sediments. Hence, young and old portions of the plant are at a similar depth, which eliminates differences in light, temperature and nutrients along the axis. To my knowledge no one has conducted studies on the periphyton of New Hampshire.

METHODS

Biweekly or monthly trips during 1975 were made to Wheelwright Pond to collect stems of *Potamogeton robbinsii* plants. The stems were carefully harvested with a garden hoe and placed gently in buckets with lake water to minimize loss of periphyton.

Two sets of leaves, with approximately equal areas, were selected

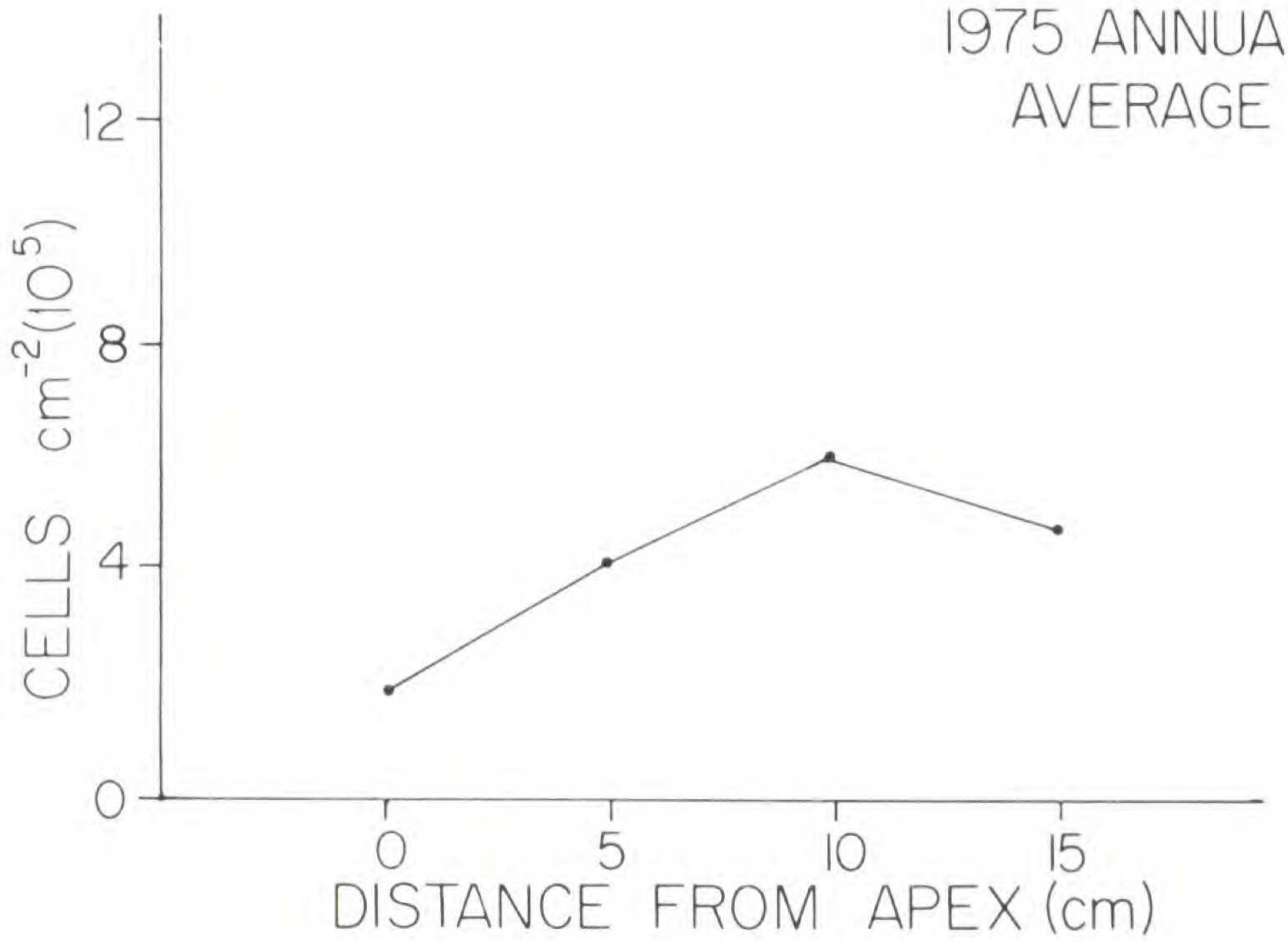

Figure 1. Average concentration of diatoms on *Potamogeton robbinsii* leaves (1975).

from at least five different randomly-chosen plants; one set was used to obtain the total surface area and the other set for quantification of diatom concentrations. From each plant two leaves were clipped at 0, 5, 10, and 15 cm. intervals from the apex and placed into separate 100 ml. beakers.

The first group of leaves was photographed and the total leaf area was determined gravimetrically. The second group of leaves was put directly through a cleaning process which oxidized all of the organics (both the leaf substrate and the diatom cell contents) leaving behind the silica frustules. Approximately 10 ml. of 50% H_2SO_4, 10 ml. of distilled water and a few crystals of potassium dichromate were placed in each beaker with the leaves and boiled for twenty minutes. After fifteen minutes a few more potassium dichromate crystals were added to insure complete oxidation of organics. After boiling, the sample was centrifuged for seven minutes at 2,500 R.P.M. Observation of the supernatant indicated no loss of diatoms. The supernatant was then removed with a specially designed vacuum decanter. The diatoms were resuspended and

washed several times with distilled water, with repeated centrifugation. After the last washing, the pellet was suspended in 8 ml. distilled water and preserved with a few crystals of thymol to prevent the growth of fungus (Patrick & Reimer, 1966).

A volume from 0.12–0.500 ml. of the oxidized sample was pipetted with a micropipette onto a number one cover slip and gently heated on a hot plate until dry, leaving the clean frustules from the known volume of the sample on the cover slip. The cover slip was inverted and mounted onto a glass slide with a drop of Kleermount mounting medium (Carolina Biological Supply). A minimum of four permanent slides was made from each sample and each was scanned under low power. The slide with the most even distribution of frustules was chosen for quantitative microscope analysis. The slide was then scanned once, twice, or until at least 1000 individual cells were identified and counted at ×1000 with a Wild M20 microscope.

Taxa were identified with the help of Hustedt (1930), Patrick and Reimer (1966, 1975), Hansmann (1973), and the Fritsch microfiche collection.

RESULTS

Along the shoot of *Potamogeton robbinsii* an increase in diatom concentration was observed from the apex to approximately 10 cm. From 10 to 15 cm. the concentration of diatoms decreased or remained approximately the same (Figure 1). At the apex the annual average was 1.9×10^5 diatoms/cm^2 while at 5 and 10 cm. from the apex the average was two and three times higher. At 15 cm. the average cell concentration was 4.7×10^5 cells/cm^2.

Monthly variations in the concentrations of epiphytes were observed (Figures 2a-d). The range in concentrations was from 0.2×10^5 at the apex on 4 June to 13.2×10^5 cells/cm^2 at 10 cm. from the apex on 5 April. Spring and fall maxima occurred from April through June and October through November, respectively. A marked decline in diatom concentrations occurred during May. A mid-summer minimum occurred between June and September. The decline in diatom concentration in the shoot section from 10 to 15 cm. did not occur during July and August. During the summer very low concentrations occurred at the apex. The concentration profile along the axis became uniform during the late winter.

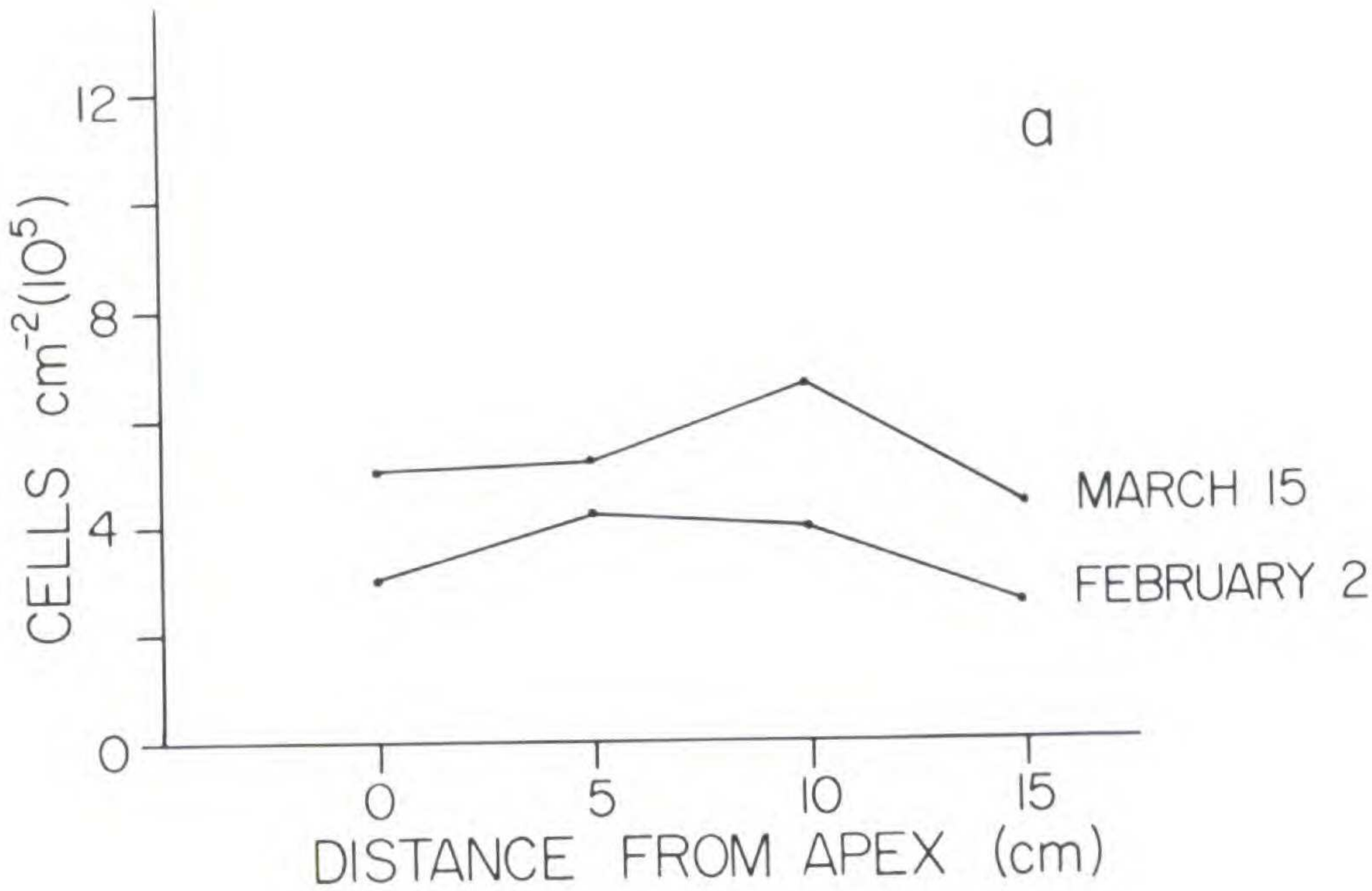

Figure 2a. Concentration of diatoms on *Potamogeton robbinsii* leaves, February 2 and March 15, 1975.

A total of 133 taxa of epiphytic diatoms were encountered (Species List). The three most abundant species were *Achnanthes minutissima, Cocconeis placentula* var. *euglypta,* and *Eunotia incisa. Anomoeoneis vitrea* was occasionally abundant. Of lesser importance were *Tabellaria fenestrata, Fragilaria capuncina* var. *mesolepta, Navicula radiosa,* and *Navicula radiosa* var. *tenella.*

Maxima and minima of the dominant epiphytic taxa occurred at various times during the year. *Achnanthes minutissima* had a maximum in the late spring (April through June) followed by a summer minimum that extended into the early fall (Figure 3a). Late in the year a smaller maximum occurred. An abrupt decrease in concentration occurred in May. The decrease was from 7.4×10^5 cells/cm^2, the largest concentration of an individual species found throughout the year, to 1.4×10^5 cells/cm^2.

Cocconeis placentula var. *euglypta* had maxima in June and November of 2.5×10^5 and 2.9×10^5 cells/cm^2 and a minimum in late September of 0.45×10^5 cells/cm^2 (Figure 3b). In these respects the seasonal pattern is similar to that of *Achnanthes minutissima.* The seasonal profiles differ in that the decrease in numbers of *C. placentula* var. *euglypta* in May was slight and its maximum values

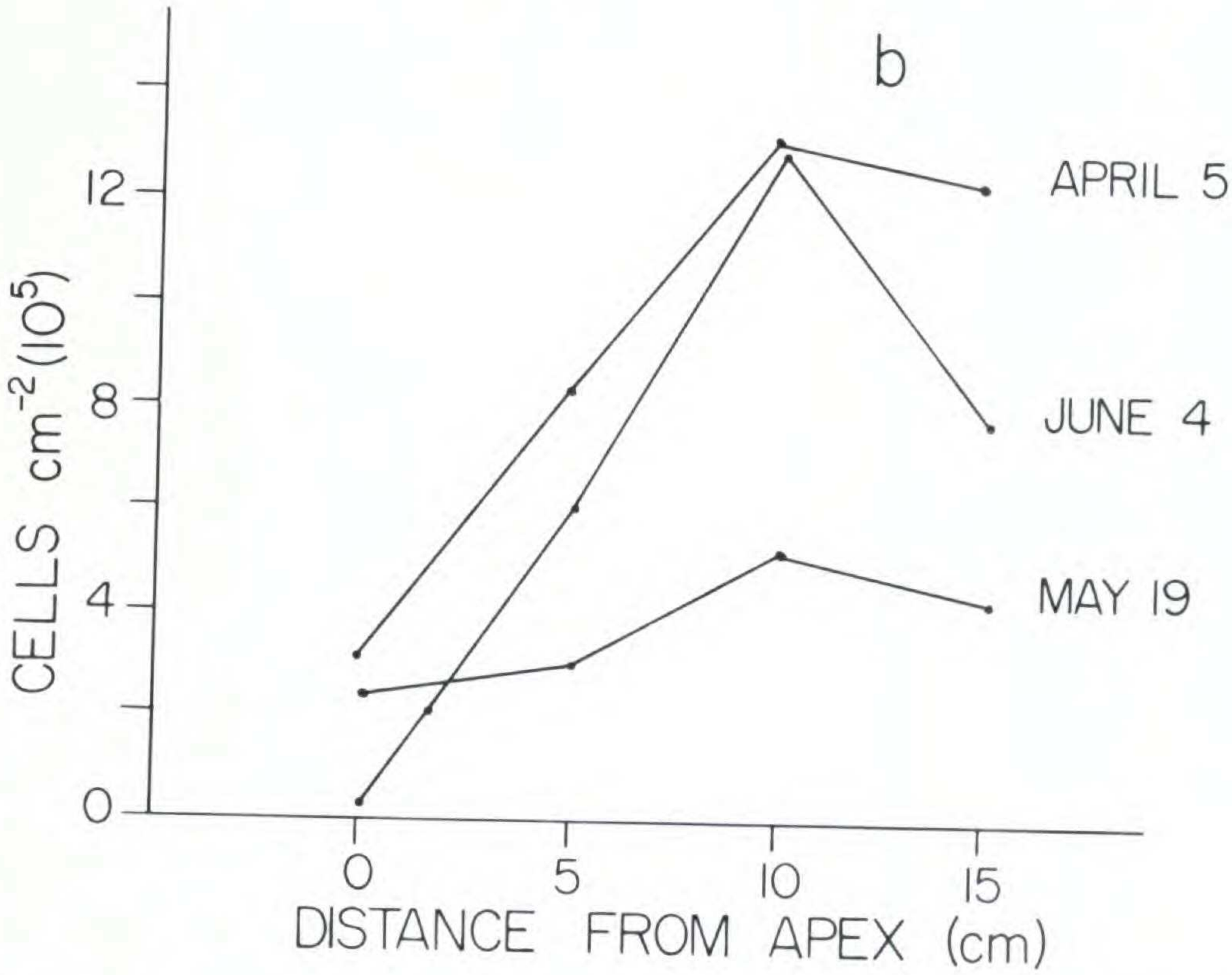

Figure 2b. Concentration of diatoms on *Potamogeton robbinsii* leaves, April 5, May 19, and June 4, 1975.

did not approach those of *A. minutissima*.

Eunotia incisa had a seasonal profile markedly similar to that of *Cocconeis placentula* var. *euglypta* (Figure 3c). Both had spring and fall maxima, a summer minimum and only a slight decline in concentration during May.

The community structure along the shoot of *Potamogeton robbinsii* varied throughout the year. During late winter (February and March) the community structure was similar from 0 to 15 cm. along the shoot (represented by March, Figure 4a). During these months no apical growth of *P. robbinsii* was observed.

During spring through late fall (April through November) distinct changes in community structure occurred along the shoot (represented by April 5, July 7 and November 22, Figures 4b, c, & d). The dominant taxa increased in concentration from 0 to 10 cm. and decreased slightly from 10 to 15 cm. Changes in dominance or relative abundance of these taxa shifted as the leaves aged. One group of two species, *Eunotia incisa* and *Cocconeis placentula* var. *euglypta*, had a parallel pattern of decreasing relative abundance

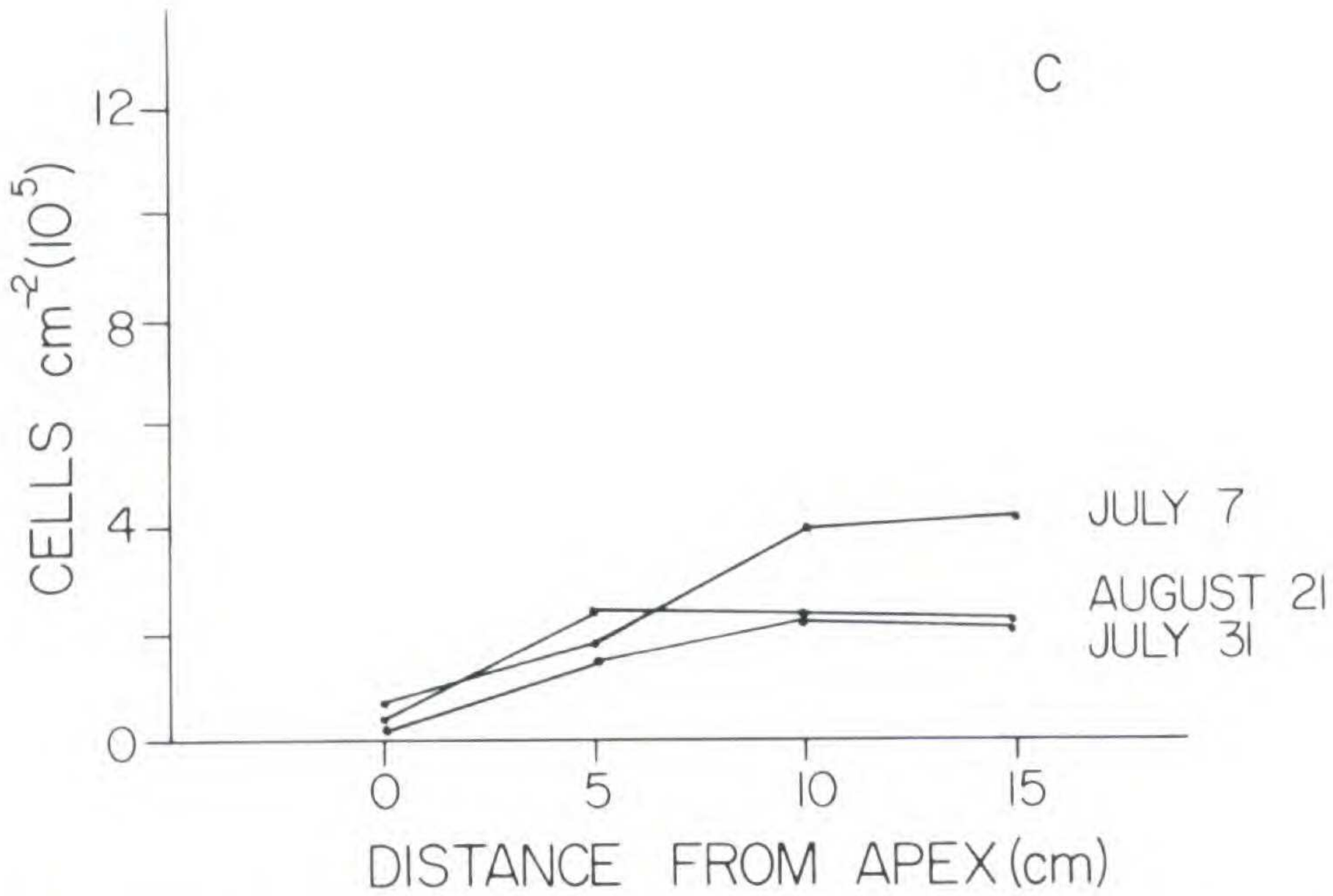

Figure 2c. Concentration of diatoms on *Potamogeton robbinsii* leaves, July 7, July 31, and August 21, 1975.

along the shoot. A second group, *Achnanthes minutissima* and *Anomoeoneis vitrea* had a parallel pattern of increasing relative abundance along the shoot. Between 10 and 15 cm., when the total number of diatoms/cm^2 decreased, a reversal of this trend occurred, i.e. the importance of *C. placentula* var. *euglypta* and *E. incisa* again increased, while that of *A. minutissima* and *A. vitrea* decreased.

Although the trends of relative abundance of *Anomoeoneis vitrea* were similar to those of *Achnanthes minutissima* the concentration was much lower. The average concentrations of *Eunotia incisa* and *Cocconeis placentula* var. *euglypta* were similar to each other.

DISCUSSION

The horizontal growth habit of *Potamogeton robbinsii* eliminates light, temperature, and depth as factors resulting in the observed changes in the epiphytic community along the shoot. Therefore, the only apparent causal factor is leaf age. As a newly formed leaf becomes exposed to the aquatic environment, algae and bacteria coat it with mucilage (Young, 1945; Patrick & Reimer, 1966). The mucilage then captures silt and particulate matter and enables other microorganisms to attach. The cumulative increase of mucilage as the leaves mature may be the primary cause of the increase of epiphytes from 0 to 10 cm.

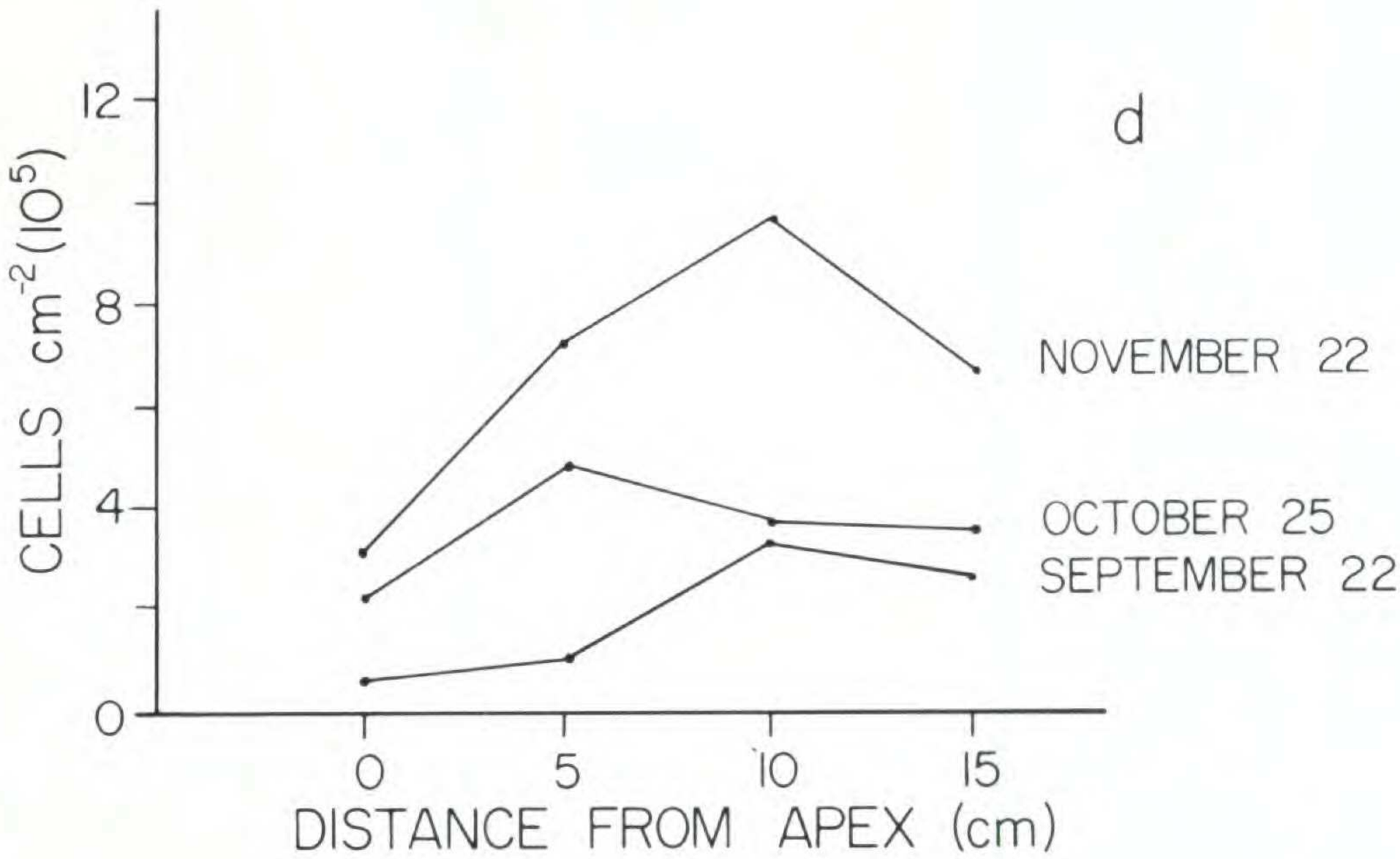

Figure 2d. Concentration of diatoms on *Potamogeton robbinsii* leaves, September 22, October 25, and November 22, 1975.

Associated with the increase in diatoms from 0 to 10 cm. was an increase in the blue-green algae on the older leaves. These algae apparently behave as successional species, requiring a mucilage layer before they become part of the periphyton. The increase in blue-green algae may also account for some of the increase in total numbers of diatoms by increasing the surface area available for attachment. Most of the blue-green algae present had thick mucilage sheaths which enabled further colonization by diatoms.

The decrease in diatom numbers between the 10 and 15 cm. level is also accountable due to the interplay of physical factors. It is apparent that for a given substrate the periphytic mat may only attain a finite size, above which a "sloughing off" occurs, enhanced by the breakdown of the macrophyte substrate. Also, fewer blue-green algae were present at the 15 cm. level, so that their loss also accounted for part of the decrease in diatoms.

Differences between the monthly distribution patterns of diatoms along the axis of the *Potamogeton robbinsii* plants (Figures 2a-d) are explained on the basis of differential growth of the macrophyte itself. For example, in February and March the distribution was relatively uniform and the macrophytes were not actively growing. As a result the diatom communities on all sections of the axis were similar in concentration. Winter environmental conditions such as

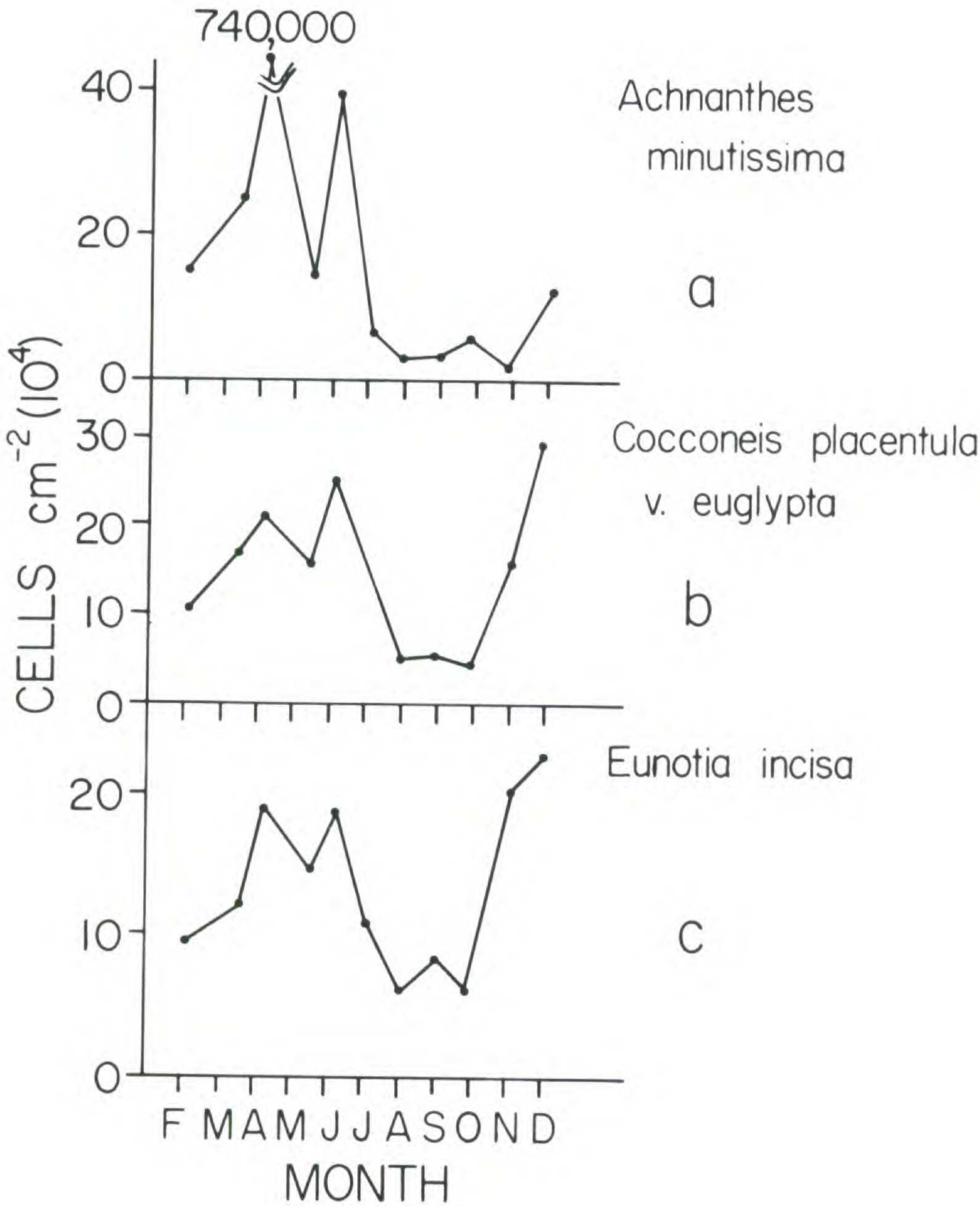

Figure 3. Seasonal concentration of dominant diatoms on *Potamogeton robbinsii*. a. *Achnanthes minutissima;* b. *Cocconeis placentula* var. *euglypta;* c. *Eunotia incisa.*

very low levels of light and temperature limited diatom concentrations to approximately one-third of the yearly maximum.

Another distribution pattern was the low concentration of epiphytes on the apical leaves relative to the concentration on older leaves during April through September. This distribution is explained on the basis of the macrophyte growth cycle. During these

months, new leaves were constantly produced by the apical meristem providing new substrate for colonization. The epiphyte community on the young leaves was always at a "pioneer" stage with low cell concentration. As the leaves aged, "successional" stages appeared. During July and August the decline in cell concentration from 10 to 15 cm. was not present; this distribution is attributable to both the high growth rate of *Potamogeton robbinsii* and to reduced degradation of leaves in that segment. In future studies the growth rate and age of the individual leaves of the macrophyte should be quantified in order to determine the specific rate of colonization by diatoms.

The seasonal fluctuations of diatoms on *Potamogeton robbinsii,* which include a large spring maximum, a summer minimum, and a small fall maximum, are in agreement with previous seasonal studies of diatoms. Most diatoms favor low light levels and temperature, and many investigators suggest that these factors are the triggering mechanisms for the spring and fall blooms (Smith, 1950; Patrick & Reimer, 1966). Such seasonal fluctuations of diatoms are similar in a variety of habitats: attached diatoms in streams (Patrick, 1948; Douglas, 1958); epilithic communities in oligotrophic lakes (Stockner & Armstrong, 1971; Fox et al., 1969); epiphytic communities in lake systems (Foerster & Schlichting, 1969; Godward, 1937); and studies of colonization of artificial substrates in river systems (Flemer, 1970; Baker, 1974).

The marked May decrease in the spring maximum in Wheelwright Pond was probably caused by increased wave action due to overturn which scoured away many of the loosely attached forms. With overturn completed by June and the growth rate of the diatoms high, large concentrations of epiphytes developed.

The similar seasonal growth curves of *Cocconeis placentula* var. *euglypta* and *Eunotia incisa* suggest that these taxa have similar environmental requirements, growth rates, and abilities to retain substrates. The decline in *Achnanthes minutissima* and *Anomoeoneis vitrea* during May was much larger than that of *C. placentula* var. *euglypta* or *E. incisa* and suggests a weaker attachment mechanism.

The ability of a diatom to attach onto a substrate helps determine whether it is a "pioneer" or "climax" species. This study shows that there are definite changes in species composition over time; there is a group of species which can cling to the freshly formed leaves while

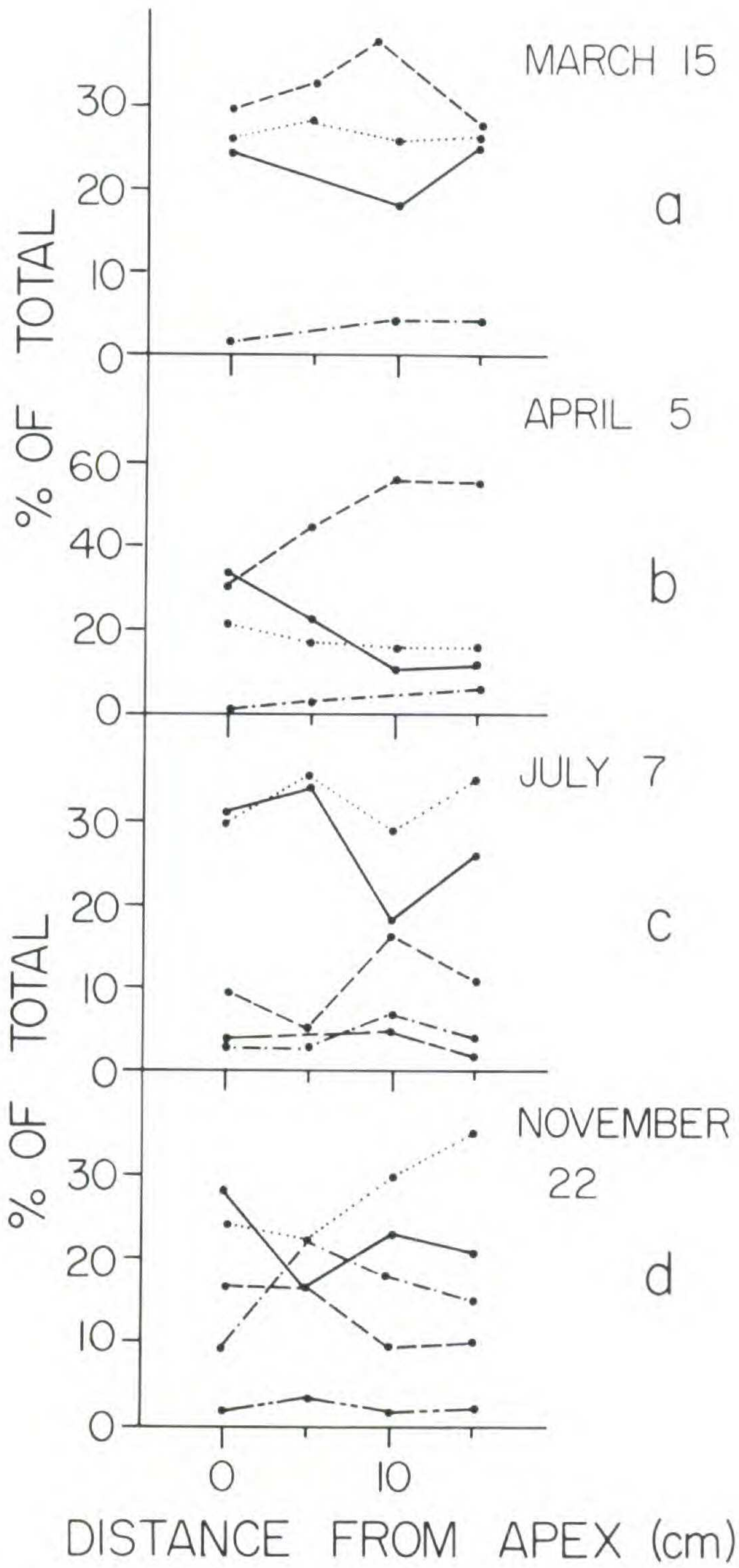

Figure 4. Relative abundance of dominant diatoms on *Potamogeton robbinsii* leaves (1975). a. March 15; b. April 5; c. July 7; d. November 22. — — — — = *Achnanthes minutissima*; ..... = *Cocconeis placentula* var. *euglypta*; ———— = *Eunotia incisa*; . — . — . — = *Anomoeoneis vitrea*; — - - — = *Tabellaria fenestra*.

other diatoms do not adhere until a mucilage layer is formed. The former group represents the "pioneers" and the latter the "climax" species.

In observing "pioneer" communities on the *Potamogeton robbinsii* leaves one should consider only those dates where growth of the substrate occurred. These were the only times that new leaves were added at the shoot apex. I found that communities at 0 cm. were primarily dominated by two species, *Eunotia incisa* and *Cocconeis placentula* var. *euglypta* (Figure 4). At the 5 and 10 cm. levels *Achnanthes minutissima* and *Anomoeoneis vitrea* became more important. A few additional species had their highest frequency at 0 cm. (the "pioneer" stage) although most of the minor species had their highest frequencies in the older communities.

Additional evidence supports the successional pattern as outlined above. First, *Eunotia incisa* and *Cocconeis placentula* var. *euglypta* were the only two species attached to newly formed leaves and represent very early "pioneer" stages. Second, it was observed that *E. incisa* and *C. placentula* var. *euglypta* had superior attachment mechanisms as they were eroded to a lesser extent than were *Achnanthes minutissima* and *Anomoeoneis vitrea* in May.

Superior attachment mechanisms for *Cocconeis placentula* var. *euglypta* and *Eunotia incisa* are evident. *Cocconeis* has a broad, flat, slightly curved morphology and secretes a layer of mucilage. Such characteristics enable it to cling firmly to substrate (Smith, 1950; Sieburth & Thomas, 1973; Stockner & Evans, 1972). *Eunotia* secretes large quantities of mucilage, has a curved symmetry, and can form filaments, all of which enable it to adhere to and entangle with fresh substrates.

Achnanthes minutissima and *Anomoeoneis vitrea* are both smaller than the other major contributors and, hence, probably have a larger specific growth rate (Fogg, 1965). This is one possible means by which *A. minutissima* and *A. vitrea* may have a higher concentration than the "pioneer" forms once they become attached in successional stages of community development.

Other workers have recorded similar successional patterns. Dillard (1969) found *Eunotia pectinalis* var. *minor* to be the "pioneer" organism of epilithic diatom communities, although the species was not dominant in the mature communities where *Achnanthes minutissima* and *Gomphonema parvulum* were codominant. Stockner and Evans (1972) observed a well defined successional pattern where

A. minutissima was most dominant in later stages of community development. Sieburth and Thomas (1973) found a *Cocconeis* species attached to eelgrass in large numbers, completely covering the plant, causing it to break down. It was not until later stages in the development of the community that other diatoms colonized the substrate.

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Species list of diatoms found on Potamogeton robbinsii leaves during 1975.

Cyclotella bodanica Eul., *C. kutzingiana* Thwaites, *C. meninginiana* Kutz., *C. stelligera* (Cleve) Grun., *C.* sp. (unknown), *Melosira distans* (Ehrb.) Kutz., *M. granulata* (Ehrb.) Ralfs., *M.* sp., *Stephanodiscus astraea* var. *minutula* (Kutz.) Grun., *Thalassiosira tumida* Hustedt, *Achnanthes affinis* Grun., *A. clevei* Grun., *A. clevei* var. *rostrata* Hustedt, *A. detha* Horn & Hellerman, *A. gibberula* Grun., *A. lanceolata* Breb., *A. lanceolata* var. *elliptica* Cleve, *A. lanceolata* var. *rostrata* Hustedt, *A. linearis* W. Sm., *A. microcephala* Kutz., *A. minutissima* Kutz., *Amphipleura pellucida* Kutz., *Amphora ovalis* Kutz., *Anomoeoneis vitrea* (Grun.) Ross, *Asterionella formosa* Hassall, *Bacillaria paradoxa* var. *tumidula* Grun., *Caloneis bacillum* (Grun.) Mereschkowsky, *Caloneis silicula* (Ehrb.) Cleve, *C. schumanniana* (Grun.) Cleve, *Cocconeis placentula* (Ehrb.) var. *euglypta* (Ehrb.) Cleve., *Cymbella aspera* (Ehrb.) Cleve, *C. cistula* (Hemprich) Grun., *C. cistula* var. *maculata* (Kutz.) Van Heurck, *C. gracilis* (Rabh.) Cleve, *C. naviculiformis* Aversw. ex Heib. Auerswald, *C. sinuata* Greg., *C. turgida* (Greg.) Cleve, *C. ventricosa* Kutz., *Diploneis marginestriata* Hustedt, *Epithemia turgida* (Ehrb.) Kutz., *Eunotia curvata* Lagerst., *E. flexuosa* Kutz., *E. flexuosa* var. *eurycephala* Grun., *E. incisa* W. Sm. ex Greg., *E. incisa* (large) W. Sm. ex. Greg., *E. major* (W. Sm.) Rabh., *E. pectinalis* (Kutz.) Rabh., *E. pectinalis* (Kutz.) Rabh. var. *minor* (Kutz.) Rabh., *E. impressa* (Ehrb.) Rabh., *E. pectinalis* var. *ventricosa* Grun., *E. serra* var. *diadema* (Ehrb.) Patr., *E. valida* Hustedt, *E. vanheurckii* Patr., *Fragilaria capucina* Desmazieres, *F. capucina* Desmazieres var. *mesolepta* (Rabh.) Grun., *F. construens* (Ehrb.) Grun., *F. crotonensia* Kitton, *F. harrissonii* W. Sm., *F. intermedia* Grun., *F. pinnata* Ehrb., *F.* sp., *F. virescens* var. *mesolepta* Rabh., *Frustulia rhomboides* (Ehr.) de Toni, *Gomphocymbella* sp., *Gomphonema acuminatum* Ehrb., *G. acuminatum* Ehrb. var. *brebissonii* (Kutz.) Clev., *G. acuminatum* Ehrb. var. *coronata* (Ehrb.) W. Sm., *G. angustatum* (Kutz.) Rabh., *G. augur* Ehrb., *G. constrictum* Ehrb., *G. constrictum*

Ehrb. var. *capitata* (Ehrb.) Cleve., *G.* sp. (girdle), *G. gracile* Ehrb., *G. gracile* Ehrb. var. *lanceolata* (Kutz.) Cleve., *G. intricatum* Kutz., *G. olivaceum* (Lyngbye) Kutz., *G. parvulum* (Kutz.) Grun., *Gyrosigma obscurum* (W. Sm.) Griff. & Henfr., *G. spencerii* (Quek.) Griff. & Henfr., *Hantzschia amphioxys* (Ehrb.) Grun. var. *virox* (Hantzsch) Grun., *Meridion circulare* Agardh, *M. circulare* Agardh var. *constricta* (Ralfs.) van Heurck., *Navicula bacillum* Ehrb., *N. cryptocephala* Kutz., *N. cuspidata* var. *ambigua* (Ehrb.) Cleve, *N. falaisiensis* Grun., *N. hungarica* var. *capitata* (Ehrb.) Cleve, *N. minima* Grun., *N. protracta* Grun., *N. pseudoscutiformis* Hustedt, *N. pupula* Kutz., *N. pupula* Kutz. var. *elliptica* Hustedt, *N. pupula* var. *rectangularis* (Greg.) Grun., *N. radiosa* Kutz., *N. radiosa* (Kutz.) var. *tenella* (Breb.) Grun., *N. rhyncocephala* Kutz., *N. tridentula* Krasske, *N. verecunda* Hustedt, *Neidium affine* (Ehrb.) Cleve, *Neidium iridis* var. *ampliata* (Ehrb.) Cleve, *Nitzschia acicularis* W. Sm., *N. acuta* Hantzsch, *N. amphibia* Grun., *N. obtusa* var. *scalpelliformis* Grun., *N. paleacea* Grun., *N. recta* Hantzsch, *N.* sp., *N. subtilis* (Kutz.) Grun., *Rhopalodia gibba* (Ehrb.) O. Mull., *Pinnularia abaujensis* (Pont.) Ross, *P. gibba* Ehrb., *P. intermedia* (Lagerst.) Cleve, *P. nodosa* (Ehrb.) W. Sm., *P.* sp.,*P. sudetica* Hilse, *Stauroneis anceps* Ehrb., *S. anceps* var. *hyalina* Brun & Peragallo, *S. anceps* Ehrb. f. *linearia* (Ehrb.) Cleve, *S. ignorata* Hustedt, *S. kriegeri* Patr., *S. livingstonii* Reim., *S. perminuta* Hustedt, *S. phoenicenteron* Ehrb., *Surirella delicatissima* Lewis, *Synedra arcus* Kutz., *S. parasitica* W. Sm., *S. pulchella* Kutz., *S. rumpens* Kutz., *S. tenera* W. Sm., *S. ulna* (Nitzsch) Ehrb., *S. vaucheriae* Kutz., *Tabellaria fenestrata* (Lyngbye) Kutz., *T. flocculosa* (Roth) Kutz., and one unidentifiable specimen.

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